



REVIEW

Sex-associated differences in sclerochronology and sensitivity to thermal stress in Caribbean and eastern Pacific reef-building corals

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ABSTRACT: The density banding patterns of the skeletons of massive reef-building corals can be used as historical records of their growth, life history, and environmental conditions. By analyzing these patterns, it is possible to estimate growth parameters such as skeletal density, extension rate, and calcification rate. The responses of stony corals to environmental stress depend on the amount of energy available for high-energetic metabolic processes, including skeletal calcification and sexual reproduction. The sex of a colony may also influence its calcification rate and resistance to environmental stressors like thermal anomalies. Here, we review and summarize the literature that focuses on sex-associated differences in coral calcification rates between male and female colonies and then we examine their differential responses to changes in sea surface temperature (SST) in *Porites panamensis*, *P. lobata*, *Pavona gigantea*, *Siderastrea siderea*, *Montastraea cavernosa*, *Dichocoenia stokesi*, and *Dengrogyra cylindrus* from the eastern Pacific and Caribbean regions through a reanalysis of published data. Differences in the calcification rates between sexes were due to the energy available for calcification and the strategy employed for skeletal growth. Female corals exhibited lower calcification rates than male colonies in all coral species. The results reveal that overall, the calcification rate was negatively related to SST when the data of both sexes were pooled. However, when data were analyzed separately by sex, only the calcification rate of females was significantly dependent on SST. These findings highlight the implications for paleoenvironmental reconstructions using coral skeletons and the potential disparities in the populations of gonochoric corals.

KEY WORDS: Coral growth · Sclerochronology · Coral calcification · Thermal stress · Sex-associated differences · Massive corals · Paleo-reconstructions · Gonochoric corals

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1. INTRODUCTION

Scleractinian corals provide the primary physical framework for coral reefs by building complex 3-dimensional structures that support what is considered the highest marine biodiversity (Perry et al. 2008, Carricart-Ganivet et al. 2012). One of the most important active processes in the bioconstruction of these 3-dimensional structures is calcification (Gattuso et al. 1998, Sheppard et al. 2009, Allemand et al. 2011), which is the sustained deposition of calcium carbonate (CaCO_3). Indeed, coral biomineralization, namely skeletal growth, is responsible for the ecological success of scleractinian corals, as it determines their ability to compete for space and resources (Lough & Barnes 2000). The balance between accretion and erosion rates controls the growth and maintenance of the reef framework at different spatiotemporal scales (Hutchings 1986, Glynn 1997, Vecsei 2004, Manzello et al. 2008). Furthermore, the inclusive records obtained from the skeletal growth of reef-building coral species provide historical climate information that can determine the resistance threshold of hermatypic corals over time (Lough & Cooper 2011).

The sclerochronological characteristics of massive coral skeletons and their inclusive records can be estimated from the density banding pattern (Knutson et al. 1972, Lough 2010), as pairs of high-density (HD) and low-density (LD) bands reflect the theoretical annual growth of the coral skeleton (Fig. 1). By analyzing the density banding pattern, 3 variables can be measured: skeletal density ($\text{g CaCO}_3 \text{cm}^{-3}$), which is the amount of carbonate deposited in a unit of volume; the extension rate (cm yr^{-1}), which is the longitudinal apical growth over 1 yr; and the calcification rate ($\text{g CaCO}_3 \text{cm}^{-2} \text{yr}^{-1}$), which results in the amount of carbonate deposited over 1 yr. These variables can be employed in a complementary manner to describe the growth (Lough & Cooper 2011) and life history of corals while making it possible to map, track, and relate coral growth to past environmental conditions.

In coral colonies with massive morphologies, the density banding pattern will arise from 2 different growth strategies depending on the skeletal

architecture of the coral species. Ceroid corals, which have porous skeletons, invest calcification resources into extending the colony linearly, whereas plocoid corals, which have solid skeletons, use CaCO_3 budgets to increase skeletal density (Carricart-Ganivet 2007, Lough & Cantin 2014). Thus, in massive plocoid corals (e.g. *Orbicella* spp.), the calcification rate is usually related to skeletal density (Cruz-Piñón et al. 2003, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020). In massive ceroid corals (e.g. *Porites* spp., *Siderastrea siderea*, and *Pavona* spp.), the calcification rate is usually related to skeletal extension (Barnes & Lough 1993, 1996, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017).

By understanding the processes and strategies that corals use to build their skeletons and quantifying sclerochronological characteristics, valuable insights into historical environmental conditions can be obtained (Lough 2010), such as those that have been gleaned by other proxy recorders like tree rings or ice cores (Barnes & Lough 1993, 1996). For example, maximum calcification rates are generally recorded when

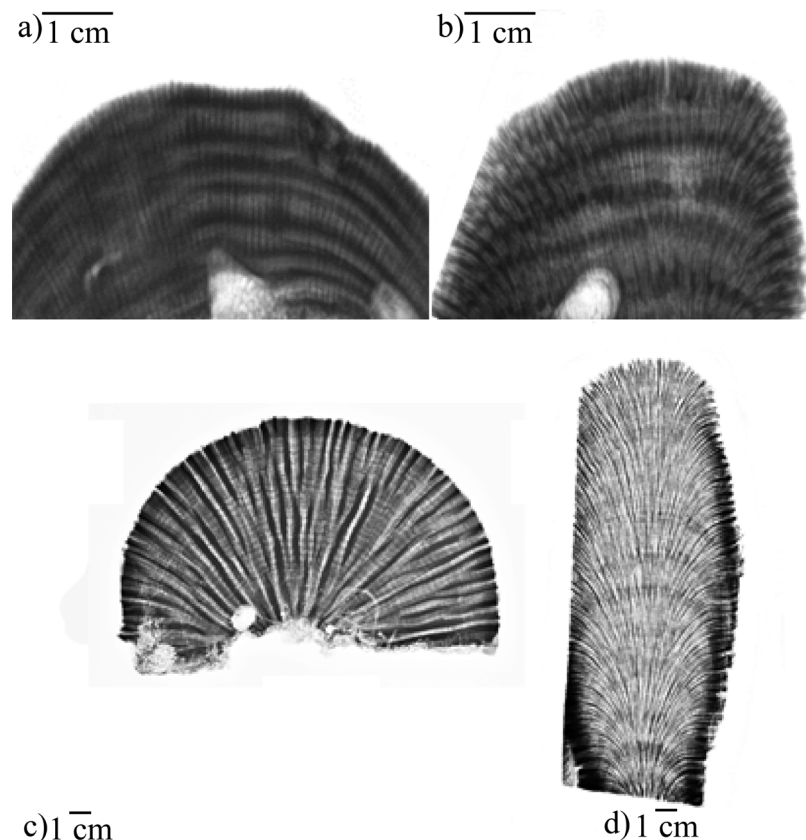


Fig. 1. X-radiograph positive images of sliced skeletons showing annual density banding pattern (dark band: high density; light band: low density) in massive corals (a) *Porites panamensis*, (b) *Pavona gigantea*, (c) *Dichocoenia stokesi*, and (d) *Dendrogyra cylindrus*

environmental conditions (e.g. temperature and irradiance) are optimal (Kleypas et al. 1999 a,b, Carricart-Ganivet 2007, Colombo-Pallota et al. 2010, Done 2011). Thus, the density banding pattern of coral skeletons can mirror the environmental variability of the area. Understandably, density banding patterns have become pertinent ecological indicators of the negative effects of climate change and the local pressures that affect coral reefs (Barnes & Lough 1996, Cohen et al. 2004, Manzello et al. 2008, Lough 2010, Manzello 2010a,b, Anthony et al. 2011, Lough & Cantin 2014).

Several environmental factors drive coral density banding patterns and/or coral calcification rates, including light irradiance, aragonite saturation, water turbidity, and hydraulic energy (Wellington & Glynn 1983, Lough & Barnes 2000, Grigg 2006, Smith et al. 2007, Lough & Cooper 2011). Sea surface temperature (SST) has been historically singled out as a key controller of coral calcification rates and all high-cost physiological processes (Lough & Barnes 2000). In most stony corals, the calcification rate is positively related to the intra-annual variability in SST during an annual cycle (Lough & Barnes 2000, Lough & Cooper 2011). However, recurrent thermal anomalies in SSTs above the seasonal average can disrupt or inhibit calcification and cause bleaching (De Salvo et al. 2008, Carilli et al. 2009), depending on the intensity and periodicity of the thermal stress and the acclimatization, resistance, local thermal history, and thermal sensitivity of the coral species present (Carricart-Ganivet et al. 2012). Long-term experiments have shown that most corals exhibit optimal calcification rates at SSTs ranging from 26–29°C, with calcification rates plummeting when thermal conditions become suboptimal ($\pm 2^\circ\text{C}$ of mean annual SST; Clausen & Roth 1975, Jokiel & Coles 1977, Coles & Jokiel 1978, Marshall & Clode 2004, Hoegh-Guldberg et al. 2007, Allemand et al. 2011, Veron et al. 2016). Indeed, decreasing calcification rates in different ecoregions have been linked to the continual abnormal increase in average annual SSTs over time (Wórum et al. 2007, Cooper et al. 2008, De'ath et al. 2009, Saenger et al. 2009, Tanzil et al. 2009, 2013, Cantin et al. 2010, Carricart-Ganivet et al. 2012, Tortolero-Langarica et al. 2017, Cruz-Ortega et al. 2020).

The responses and resilience of stony corals to environmental stress depend on their life histories and the amount of energy available to cope with stress and maintain key metabolic processes such as tissue formation, tissue repair and maintenance, reproduction, and skeleton calcification (Leuzinger et al. 2003, Grottoli et al. 2006, Rodrigues et al. 2008, Harrison 2011, Tambutté et al. 2011). In stony corals, calcifica-

tion occurs in partial isolation from the surrounding seawater in the calciblastic epithelium, resulting in a thin layer of living tissue at the surface of the colony (Cohen & McConnaughey 2003, Cohen & Holcomb 2009). Corals can control the chemical conditions of the calciblastic epithelium by actively transporting hydrogen ions out of or into the calcifying fluid, which are energetically expensive processes that are fueled by coral–algae symbiosis (Barnes & Lough 1993, Cohen & McConnaughey 2003, Cohen & Holcomb 2009, Colombo-Pallotta et al. 2010).

Both coral calcification and reproduction are highly energetically demanding processes, with at least 30 and 25% of the energy budget invested in calcification (Allemand et al. 2011) and gamete maturation (Richmond 1987, Rinkevich 1989, Leuzinger et al. 2003), respectively. Indeed, reproduction may be a key factor that affects coral growth, especially in gonochoric species, as it is more energetically costly to produce eggs than sperm (Ward 1995a,b, Hall & Hughes 1996, Leuzinger et al. 2003). Therefore, calcification rates in gonochoric corals differ between sexes due to the amount of energy that is diverted away from calcification to reach the energetic demands of reproduction (Rinkevich 1989, Leuzinger et al. 2003, Cabral-Tena et al. 2013, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020). The sex of the coral colony may also influence its sensitivity and response to environmental stressors that affect calcification (e.g. thermal stress and ocean acidification), which can disrupt the sex ratio of the population and affect the demographics of coral species. Indeed, this outcome has been identified in *Astrangia poculata* under laboratory conditions (Holcomb et al. 2012) and in *Dichocoenia stokesi* and *Dendrogyra cylindrus* under natural conditions (Cruz-Ortega et al. 2020). Other problems may also arise if colony sex is disregarded in ecological and sclerochronological studies, including biased coral growth estimations and the inappropriate use or misinterpretation of the information obtained from corals when they are used as environmental proxies (Cabral-Tena et al. 2013, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2017).

Our objectives for this review are to highlight sex-associated differences in sclerochronological characteristics and calcification rates, especially in response to changes in SST. This review includes studies conducted with 7 massive coral species with ceroid or plocoid skeletal architectures from 2 oceanographically contrasting environments: the Caribbean Sea and the Eastern Tropical Pacific Ocean (ETP).

2. SEX-ASSOCIATED DIFFERENCES IN CORAL GROWTH

To date, 6 studies have reported sex-associated differences in the sclerochronological characteristics of 7 hermatypic coral species from the Caribbean and ETP regions (Cabral-Tena et al. 2013, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020). This persistent pattern in gonochoric stony corals has been reported in species with both ceroid and plocoid skeletal architectures, different reproduction strategies (e.g. brooding or broadcast spawning), and seasonal and annual egg maturation (Table 1).

The sex-associated differences in the sclerochronological characteristics of stony corals have reflected the following patterns. Female colonies have lower calcification rates than those of males in all analyzed species and regions, except *Siderastrea siderea* (Fig. 2a). The extension rate was found to be higher in male colonies, although it was similar between sexes in *Pavona gigantea*, *Dendrogyra cylindrus*, and *Montastraea cavernosa* (Fig. 2b). Skeletal density was higher in male colonies of *P. gigantea*, *D. cylindrus*, and *M. cavernosa* than in female colonies yet equivalent between sexes in the other 4 species (Fig. 2c). These sex-associated differences in sclerochronological characteristics can be explained by considering 2 main components of skeletal formation: (1) the energy available for calcification (Fang et al. 1989, Colombo-Pallotta et al. 2010), some of which will be invested into egg maturation in female colonies; and (2) the strategy employed to construct the CaCO₃ skeleton, with some corals growing quickly and others forming dense structures (Carricart-Ganivet & Merino 2001).

2.1. Energy budget devoted to calcification are different between sexes

The sex-based difference in the energetic budget for calcification reflects the amount of energy allocated to physiological processes, which varies (Rinkevich 1996, Allemand et al. 2011, Leuzinger et al. 2012) and is related to whether the source of energy was obtained through autotrophic or heterotrophic routes (Cohen & Holcomb 2009). It has also been reported that the reallocation of resources from calcification to sexual reproduction can inhibit coral growth (Richmond 1987, Leuzinger et al. 2003, Mendes 2004), which is notable because corals spend $\geq 25\%$ of their energy budget on reproductive processes (Richmond 1987, Rinkevich 1989, Leuzinger et al. 2003, Sheppard et al. 2009). Given that eggs are more energetically costly to produce than sperm (Harrison 1985, Hall & Hughes 1996, Harrison 2011), gonochoric female colonies invest a higher proportion of their energy budgets in gametogenesis, which leaves less energy available for calcification.

Interestingly, of the 7 coral species from the Caribbean and ETP regions, *P. gigantea* is the only one to exhibit mixed reproduction mode. In this species, the sclerochronological characteristics of hermaphroditic colonies were not statistically different from male colonies but were different from those of female colonies (Tortolero-Langarica et al. 2017). In addition, *P. gigantea* shows sequential cosexuality, with hermaphroditic colonies preferentially becoming gonochoric males rather than females in subsequent reproductive periods (Ghiselin 1969, Leonard 2006, Harrison 2011). These gonochoric male *P. gigantea* colonies show higher growth rates than those of female colonies while still being able to mature both gametes (Leonard 2006, Santiago-Valentín et al. 2015).

Table 1. Massive coral species that exhibit sex-related differences in sclerochronological characteristics

| Species | Region | Skeletal architecture | Reproductive strategy | Egg maturation | Study |
|------------------------------|-----------------|-----------------------|-----------------------|------------------|--|
| <i>Porites panamensis</i> | Eastern Pacific | Ceriod | Brooder | Several per year | Cabral-Tena et al. (2013), Tortolero-Langarica et al. (2017) |
| <i>Porites lobata</i> | Eastern Pacific | Ceriod | Broadcaster | Several per year | Tortolero-Langarica et al. (2016) |
| <i>Pavona gigantea</i> | Eastern Pacific | Ceriod | Broadcaster | Several per year | Tortolero-Langarica et al. (2017) |
| <i>Siderastrea siderea</i> | Caribbean | Ceriod | Broadcaster | Once per year | Carricart-Ganivet et al. (2013) |
| <i>Montastraea cavernosa</i> | Caribbean | Plocoid | Broadcaster | Once per year | Mozqueda-Torres et al. (2018) |
| <i>Dichocoenia stokesi</i> | Caribbean | Plocoid | Broadcaster | Once per year | Cruz-Ortega et al. (2020) |
| <i>Dendrogyra cylindrus</i> | Caribbean | Plocoid | Broadcaster | Once per year | Cruz-Ortega et al. (2020) |

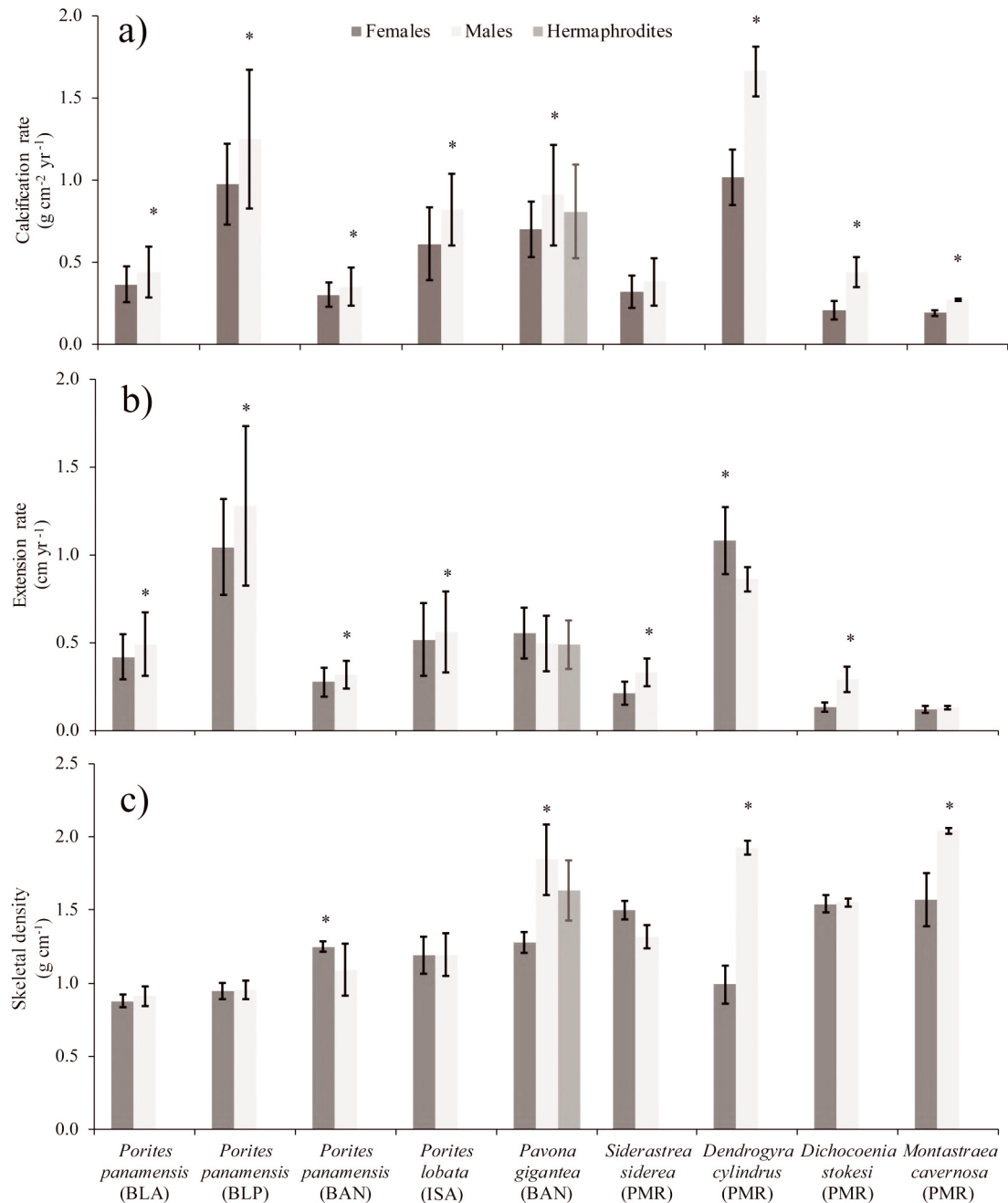


Fig. 2. Coral growth parameters (mean \pm SD) (a) calcification rate, (b) extension rate, and (c) skeletal density of gonochoric (male–female) and hermaphroditic coral species. BLA: Bahía de Los Ángeles; BLP: Bahía de La Paz; ISA: Isla Isabel; BAN: Bahía de Banderas; PMR: Puerto Morelos. Asterisks (*) denote significant differences between sexes ($p < 0.05$). Data collected from Cabral-Tena et al. (2013), Carricart-Ganivet et al. (2013), Tortolero-Langarica et al. (2016, 2017), Mozqueda-Torres et al. (2018), and Cruz-Ortega et al. (2020)

2.2. Skeletal architecture

Some clarifications are needed to explain the sex-associated differences in sclerochronological characteristics when considering skeletal bioconstruction and the growth strategies of coral species. As pre-

viously mentioned, SST is one of the most important drivers of coral calcification, with HD and LD bands associated with warm and cold seasons, respectively (Lough & Barnes 2000, Carricart-Ganivet 2004, Marshall & Clode 2004, Edmunds 2005). However, density banding patterns also depend on the skeletal archi-

texture of coral colonies and follow 2 patterns. In plocoid corals (e.g. *Montastraea*, *Orbicella*, *Dichocoenia*, and *Dendrogyra*), density banding arises from the different amounts of CaCO_3 that are deposited at different times of the year. In these cases, HD-band deposition occurs almost immediately during the summer (Dodge et al. 1993, Helmle et al. 2000, Dávalos-Dehullu et al. 2008). In ceroid corals (e.g. *Porites*, *Pavona*, and *Siderastrea*), the live tissue layer penetrates the existing skeleton, and the density banding pattern results from skeletal thickening that occurs throughout this layer. Thus, a difference is present between the actual and apparent time difference (ATD) of HD-band formation that depends on the thickness of the live tissue layer and skeletal extension rate (Barnes & Lough, 1993, 1996, Taylor et al. 1993), which can lead to errors in seasonal-band dating.

Interestingly, there is strong evidence that the skeletal architecture defines not only the density banding pattern but also the strategies that the corals use to construct their skeletons (Barnes & Lough 1993, Carricart-Ganivet & Merino 2001, Carricart-Ganivet 2007, 2011). Ceroid corals (e.g. *Porites*, *Pavona*, and *Siderastrea*) invest calcification resources into linear extensions of the colony to grow quickly; thus, any reduction in the calcification rate will lower the extension rate rather than annual skeletal density (Lough & Barnes 2000, Lough 2008). On the other hand, plocoid corals (e.g. *Montastraea*, *Orbicella*, *Dendrogyra*, and *Dichocoenia*) use CaCO_3 to augment skeletal density; thus reductions in the calcification rate decrease the resulting annual skeletal density (Carricart-Ganivet 2004, 2007, 2011, Dávalos-Dehullu et al. 2008, Lough 2008, Lough & Cantin 2014). Furthermore, coral colonies display high growth plasticity, which is related to their morphotype (e.g. massive, sub-massive, columnar, encrusting, or corallith), in response to local environmental conditions, which can even be apparent in the same reef (Lough & Barnes 2000, Lough & Cooper 2011, López-Pérez 2013). This variability results in different growth parameters among morphotypes of the same species (Norzagaray-López et al. 2015, Tortolero-Langarica et al. 2016). Therefore, differences in the sclerochronological characteristics attributed to the sex of coral colonies can also be explained by their growth strategies or construction mechanisms.

Four species that exhibit sex-associated differences in sclerochronological characteristics between sexes (i.e. *Porites panamensis*, *P. lobata*, *Pavona gigantea*, and *S. siderea*) construct porous skeletons (Table 1). Of these, *P. panamensis*, *P. lobata*, and *P. gigantea* are

distributed in the ETP, while *S. siderea* is distributed in the Caribbean. Unsurprisingly, lower extension rates explained lower calcification rates in females (Fig. 2). The lower extension rates of the female colonies compared to those of the male colonies may limit the ability of these female colonies to compete for space within reefs (Lough & Barnes 2000, Lough 2008); the only species that did not follow this pattern was *P. gigantea*, whose low calcification rates (females vs. males and hermaphrodites) were linked with low skeletal density and not low extension rates. Even though *P. gigantea* skeletons are classified as porous given that they lack exotheca and exothecal dissepiments because corallites share walls, the sclerochronological characteristics of *P. gigantea* skeletal density relate to each other as they would in solid skeletons. Thus, *Pavona* spp. corals may build highly dense skeletons as a strategy to persist in reef communities in the long term, resisting breakdown and other mechanical or chemical stressors by maintaining normal calcification rates under conditions of low aragonite saturation (Manzello 2010b).

The other 3 species that have shown sex-associated differences in sclerochronological characteristics have solid skeletons (i.e. *M. cavernosa*, *Dichocoenia stokesi*, and *Dendrogyra cylindrus*; Table 1) and are distributed in the Caribbean region. The lower calcification rate in females was expected and is explained by lower skeletal density, which is consistent with the theory of the stretching modulation of skeletal growth proposed by Carricart-Ganivet & Merino (2001). Both *M. cavernosa* and *D. cylindrus* follow this pattern (Fig. 2), but surprisingly, sub-massive *D. stokesi* corals did not, which may be related to colony morphology. Indeed, coral morphology is an important factor that influences how sclerochronological characteristics respond to environmental conditions (Tortolero-Langarica et al. 2016). An alternative explanation for this divergence from the expected relationship observed with *D. stokesi* is the sample size (3 female and 2 male colonies) employed by Cruz-Ortega et al. (2020). However, male colonies tended to have denser skeletons than female colonies (Fig. 2), resulting in these female colonies being more susceptible to physical, chemical, and biological breakdown (Carricart-Ganivet 2004, 2011).

2.3. Sex-associated differences in the calcification rate between sexes by skeleton type

Using published data (Cabral-Tena et al. 2013, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al.

2016, 2017, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020), we analyzed and evaluated the difference (%) in coral calcification rates between sexes by skeleton type. In ceroid corals (4 species), the calcification rate of male colonies was higher than that of female colonies (mean \pm SD: $20.53 \pm 2.26\%$). Likewise, in plocoid corals (3 species), the calcification rate of male colonies was higher than that of female colonies ($39.68 \pm 5.95\%$) (Fig. 3). These observed differences were significant (Student's *t*-test for uneven variances: $t_6 = -3.3849$, $p = 0.01$) and may be related to architectonic skeletal differences between plocoid and ceroid skeletons. Plocoid corals

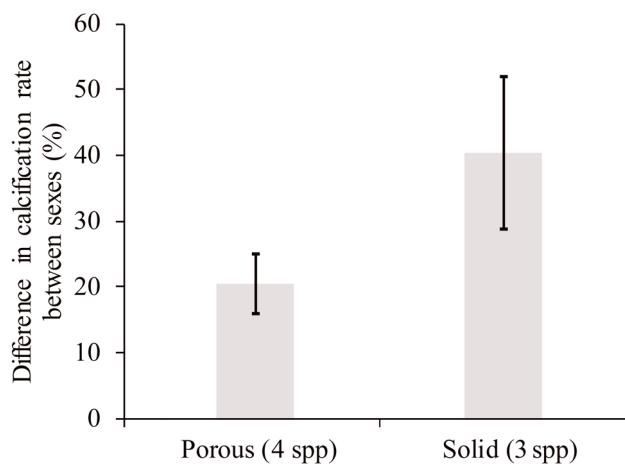


Fig. 3. Difference (%) in the calcification rates (\pm SD) between sexes by skeleton type (porous—ceroid vs. solid—plocoid). Data sets collected from Cabral-Tena et al. (2013), Carricart-Ganivet et al. (2013), Tortolero-Langarica et al. (2016, 2017), and Cruz-Ortega et al. (2020)

construct solid skeletons; thus, density banding results from different amounts of thickening deposited over skeletal structures laid down at different times of the year, and HD-band deposition is immediate, forming during the summer (Dávalos-Dehullu et al. 2008, Carricart-Ganivet et al. 2013). In contrast, the live tissue layer of ceroid corals is under the skeleton surface, which allows for continuous calcification under the tissue layer but results in delayed skeletal growth (Barnes & Lough 1992, 1993). This is important for HD band formation and the apparent timing of skeletal density bands in ceroid corals (Carricart-Ganivet et al. 2013); furthermore, it will also affect the energetic cost of skeleton formation and/or tissue maintenance in both skeleton types and explains why it is more energetically expensive to build solid skeletons (as more CaCO_3 is needed to build the skeleton), which results in greater differences in calcification rates among plocoid corals. However, this hypothesis deserves future study and proper scrutiny.

2.4. Tissue thickness

The thickness of the tissue layer (TTL) in female corals has been reported to be lower than in male corals (Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017, Mozqueda-Torres et al. 2018). Thus, the apparent sex-related differences in the TTL may be present in most gonochoric scleractinian corals (Figs. 4 & 5).

It is important to emphasize that the quantity of energy required for tissue production and repair is

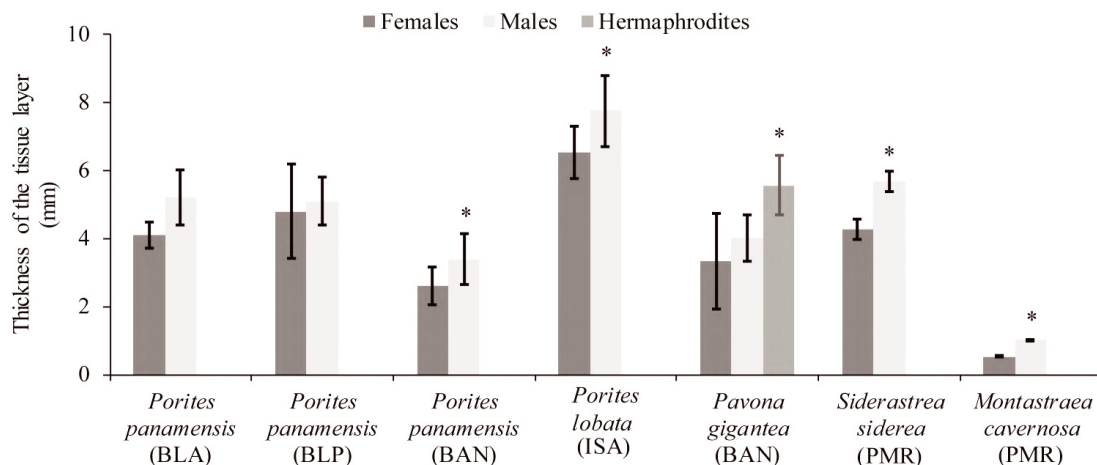


Fig. 4. Thickness of the tissue layer (mean \pm SD) of male, female, and hermaphrodites of massive coral species with documented differences in sclerochronological characteristics between sexes. BLA: Bahía de Los Ángeles; BLP: Bahía de La Paz; ISA: Isla Isabel; BAN: Bahía de Banderas; PMR: Puerto Morelos. Asterisks indicate significant differences between sexes ($*p < 0.05$). Data obtained from Cabral-Tena et al. (2013), Carricart-Ganivet et al. (2013), Tortolero-Langarica et al. (2016, 2017), and Mozqueda-Torres et al. (2018)

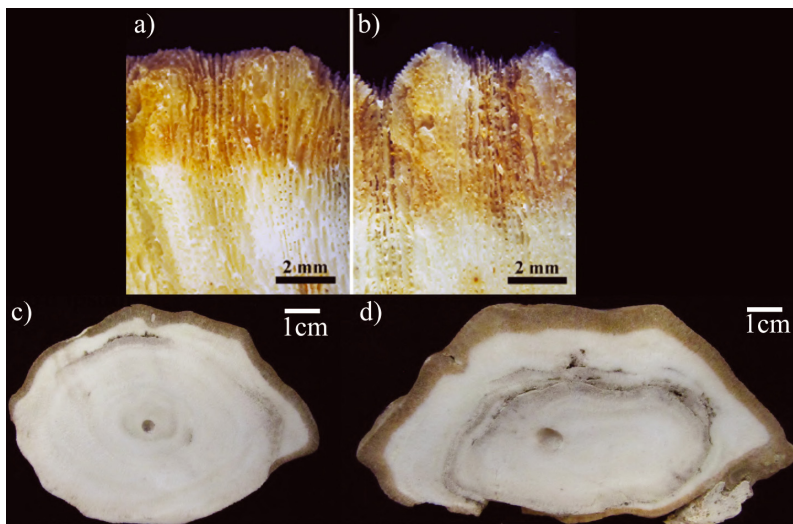


Fig. 5. Images of coral slices displaying longitudinal sections and the penetration of tissue thickness in massive species (a) *Siderastrea siderea* female colony, (b) *S. siderea* male colony (modified from Carricart-Ganivet et al. 2013), (c) *Porites lobata* female colony, and (d) *P. lobata* male colony. Note the deeper penetration of the living tissue layer in the male skeletons of both species

equivalent to the energy required for gamete production and/or embryo development (Szmant 1986, Leuzinger et al. 2003) and that the TTL is greater when conditions are favorable for coral calcification (Barnes & Lough 1992, Cruz-Piñón et al. 2003). Thus, the difference in the TTL between sexes can also be explained in terms of the energy expenditure of each sex. In females, less energy is available for tissue production after factoring in the energetic cost of gamete production than in males, which is similar to the pattern observed with sclerochronological characteristics. Nonetheless, the TTL is not often reported in studies, but it can be used as a water quality bioindicator (Cooper et al. 2008) and stress indicator for coral colonies (Barnes & Lough 1999), as it varies with sedimentation and nutrient availability (True 1995). Thus, the sex of the coral colony must be considered to use the TTL as an effective and reliable bioindicator. In addition, TTL in corals with porous skeletons is highly relevant, as density banding arises from thickening of the skeleton throughout the depth reached by the living tissue layer due to the perforate nature of their skeletons; consequently, there is a difference between the actual and apparent timing of the high-density band formation (i.e. ATD). The studies of Carricart-Ganivet et al. (2013) and Tortolero-Langarica et al. (2016, 2017) describe that the ATD

also differs between sexes of coral colonies, with a higher ATD in males than females (Table 2).

3. SEX OF THE COLONY AND PALEOENVIRONMENTAL RECONSTRUCTIONS

As coral skeletons have the potential to be environmental proxies in tropical environments, sex-associated differences in sclerochronology under natural environmental conditions have considerable implications for the interpretation of such records in paleoenvironmental reconstructions, which has been pointed out repeatedly in every study addressing these differences (Cabral-Tena et al. 2013, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020). Carricart-Ganivet et al. (2013) were the first to point this feature out when discussing that the lowest Sr/Ca values in *Siderastrea siderea* (i.e. summer) were recorded in the LD and HD bands of the female and male colonies, respectively. In that study, an ATD of density band formation of 6 mo in HD band formation was observed between sexes due to differences in the TTL and extension rate; that is, a higher ATD in males than in females. Skeletal Sr/Ca records in corals are negatively correlated with SST (Shen et al. 1996), and Sr/Ca palaeothermometry overestimates changes in SST given that their records are affected during skeletogenesis within the living tissue layer (Gagan et al. 2012). Thus, any Sr/Ca time series performed with coral species that exhibit sex-associated differences in the ATD of density band formation may provide inaccurate information if the HD band corresponds

Table 2. Sex-related differences in the apparent time difference (ATD) of density band formation. The *Pavona gigantea* hermaphrodites were considered to be male, as they showed similar ATD values

| Species | ATD females | ATD males | Study |
|----------------------------|-------------|-----------|-----------------------------------|
| <i>Porites panamensis</i> | 5 mo | 7 mo | Tortolero-Langarica et al. (2017) |
| <i>Porites lobata</i> | 5 mo | 11 mo | Tortolero-Langarica et al. (2016) |
| <i>Pavona gigantea</i> | 3 mo | 6 mo | Tortolero-Langarica et al. (2017) |
| <i>Siderastrea siderea</i> | 9 mo | 16 mo | Carricart-Ganivet et al. (2013) |

to high temperatures (i.e. summer) in females. This would lead to an overestimation of SST based on male records, and an error in the interpretation of the SST record and HD band formation in females (Carricart-Ganivet et al. 2013).

More recently, sex-associated variations in the isotopic composition (i.e. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) of *P. panamensis* skeletons were identified (Cabral-Tena et al. 2016), in which $\delta^{18}\text{O}$ was higher in female colonies than in male colonies (0.31‰ difference) whereas $\delta^{13}\text{C}$ was lower in female colonies than in male colonies (0.28‰ difference; Cabral-Tena et al. 2016). The authors mention that when isotopic data of both sexes were pooled together, the differences between the isotopic records were 0.38‰ in the ^{18}O record and 0.29‰ in the ^{13}C record. However, when data were split by sex, the differences in the isotopic records between colonies of the same sex dropped to 0.07‰ in ^{18}O and to 0.02‰ in ^{13}C , meaning that the sex of the colony explains 81 % (^{18}O) and 93 % (^{13}C) of the differences in the 'vital effect' (i.e. coral skeletons contain appreciable amounts of carbon and oxygen in isotopic disequilibrium in comparison to inorganic aragonite precipitated under isotope equilibrium due to kinetic variations attributed to differences in coral growth rate) of coral colonies.

The authors highlight that these differences in skeletal $\delta^{18}\text{O}$ could introduce an error in SST estimates of $\sim 1.0^\circ$ to $\sim 2.6^\circ\text{C}$, as faster-growing corals show depleted levels of $\delta^{18}\text{O}$ and enriched levels of $\delta^{13}\text{C}$ compared to those of slower-growing corals (i.e. the vital effect; McConnaughey 1989, Felis et al. 2003). Cabral-Tena et al. (2016) attributed their findings to differences in the vital effect that were associated with differential growth rates between colonies of different sexes and the role of Ca-ATPase, an enzyme strongly associated with coral calcification in the mechanism of the 'vital effect' because of the pH gradient that the enzyme establishes between the coral cell wall and the extracellular calcifying fluid (Adkins et al. 2003, Rollion-Bard et al. 2003). Cabral-Tena et al. (2016) theorized that higher activity of the Ca-ATPase enzyme in male corals due to a higher energy availability for calcification results in carbon-heavier skeletons and oxygen-lighter skeletons in comparison to female skeletons. Although these findings are based on one gonochoric brooding species (i.e. *P. panamensis*), their implications should be considered when climate conditions are estimated based on comparisons of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in commonly used gonochoric spawning species such as *P. lutea* and *P. lobata*.

4. SENSITIVITY OF THE CALCIFICATION RATE TO THERMAL STRESS AND SEX OF THE COLONY: CLIMATE CHANGE COULD DISRUPT THE POPULATION STRUCTURE OF GONOCHORIC STONY CORAL SPECIES

Extrinsic factors, such as SST anomalies, light supersaturation, variations in pH, and high sedimentation rates, can decrease the energy available for gamete maturation (Szmant & Gassman 1990, Glynn 1993) and affect sclerochronological characteristics depending on the thermal sensitivity and thermal life-history of the species (Jokiel & Guinther 1978, Barnes & Lough 1992, 1993, Mendes & Woodley 2002, Dávalos-Dehullu et al. 2008, Carpizo-Ituarte et al. 2011, Carricart-Ganivet et al. 2012). Corals that live in sub-optimal conditions may not produce or assimilate enough energy to complete gametogenesis and/or calcify 'healthy' skeletons (Rodrigues et al. 2008, Cohen & Holcomb 2009). For example, in some species (e.g. *Orbicella*), an annual doublet (2 narrow HD bands) in the HD band forms as temperature rises and oscillates around the optimal calcification temperature (Wórum et al. 2007, DeCarlo & Cohen 2017). The resulting stress-band signature has been reported as clear evidence of thermal stress in various coral species in the Great Barrier Reef (Cooper et al. 2008, De'ath et al. 2009, 2012), Thailand (Tanzil et al. 2009, 2013), Palau (DeCarlo & Cohen 2017), the Red Sea (Cantin et al. 2010), the Caribbean (Carricart-Ganivet et al. 2012), and the ETP (Tortolero-Langarica et al. 2017, 2022).

The responses and resistance of stony corals to environmental stress depend on the energy budget provided by the endosymbiont and bacterial core for key metabolic processes, such as calcification (Cohen & Holcomb 2009, Allemand et al. 2011), gamete and/or larval development (Szmant 1986, Leuzinger et al. 2003), and tissue production (Barnes & Lough 1992, 1999, Cruz-Piñón et al. 2003). Thus, if coral energy budgets and energy allocation are associated with colony sex, as can be seen in coral growth and TTL, a differential response to environmental stress between sexes could potentially disrupt the sex ratio and demographics of populations and species. To date, only 2 studies have addressed a differential response to environmental pressure between sexes.

First, Holcomb et al. (2012) found a negative synergic effect due to an increase in SST and $p\text{CO}_2$ on the calcification rate and reproduction of *Astrangia poculata*, an azooxanthellate coral, under experimental conditions. Interestingly, Holcomb et al. (2012) described higher sensitivity to increasing SST and $p\text{CO}_2$

in the growth and reproduction of female colonies than male colonies, suggesting a less visible long-term impact of climate change on the population structure and reproduction. Later, Cruz-Ortega et al. (2020) found that the calcification rates of *Dichocoenia stokesi* and *Dengrogyra cylindrus* were negatively correlated with SST when the data of both sexes were pooled. However, when the data sets were analyzed separately by sex, only the female colonies of both species showed a significant dependence of the calcification rate on SST (Cruz-Ortega et al. 2020). This finding suggests that climate change may impact each sex differently due to a combination of sex-dependent physiological mechanisms.

Divergent perspectives emerge when examining the information provided herein: (1) regionalization is present in the response of coral growth to extrinsic factors, and (2) the level of the response of coral growth to extrinsic factors may be local and not necessarily regional. Thus, considering that extrinsic factors may be responsible for some of the variability in the sclerochronological characteristics of corals, depending on their thermal sensitivity, thermal history of the species, and sex of the colony, we replicated the analyses reported by Cruz-Ortega et al. (2020) for the data sets of Cabral-Tena et al. (2013), Carricart-Ganivet et al. (2013), and Tortolero-Langarica et al. (2016, 2017) (Table 3); that is, we used the published yearly averaged calcification rate data and yearly SST and fitted them into some simple linear regressions using

3 models per data set: one using the yearly average female calcification rates data, another using the yearly average male calcification rates data, and the last one using the yearly average calcification rates data including both sexes (Table 4). We found the same tendency for all analyzed species, considering their distributions. The calcification rate was negatively related to SST when the data of both sexes were averaged; still, when data sets were analyzed separately by sex, only the calcification rate of female colonies was significantly dependent on SST in all cases (Fig. 6, Table 4); i.e. we reached the same conclusions as Cruz-Ortega et al. (2020) using other data sets. Interestingly, a series of ANCOVA analyses showed that the dependence of calcification on SST (slope) varied among sites and species ($p < 0.05$ in all cases; Table 4), as has been previously reported (Carricart-Ganivet et al. 2012, Norzagaray-López et al. 2015, Tortolero-Langarica et al. 2016, 2017).

The results from these analyses support the observations of Cruz-Ortega et al. (2020) and provide novel information regarding the differential response of stony corals to climate change among the sexes. For example, the calcification rate of female corals is more sensitive to changes in SST than that of males, which appears to be a common pattern in gonochoric scleractinian corals. The same patterns were obtained with data sets of several coral species collected in different sites and reef areas that included corals with different skeletal architectures and growth strategies,

Table 3. Metadata of data sets used in the analysis of the mean annual calcification rates as a function of the average annual sea surface temperature

| Species | Site (coordinates) | No. of female colonies | No. of male colonies | Growth years reconstructed | Study |
|------------------------------|--------------------------------------|----------------------------|----------------------|----------------------------|-----------------------------------|
| <i>Porites panamensis</i> | Bahía de Los Ángeles (29° N, 113° W) | 5 | 5 | 1996–2010 | Cabral-Tena et al. (2013) |
| <i>Porites panamensis</i> | Bahía de La Paz (24° N, 110° W) | 4 | 6 | 1998–2010 | Cabral-Tena et al. (2013) |
| <i>Porites panamensis</i> | Islas Marietas (20° N, 105° W) | 1 | 3 | 2003–2012 | Tortolero-Langarica et al. (2017) |
| <i>Porites lobata</i> | Isla Isabel (21° N, 105° W) | 3 | 3 | 2007–2013 | Tortolero-Langarica et al. (2016) |
| <i>Pavona gigantea</i> | Islas Marietas (20° N, 105° W) | 1 Female, 2 hermaphrodites | 2 | 1988–2012 | Tortolero-Langarica et al. (2017) |
| <i>Siderastrea siderea</i> | Puerto Morelos (20° N, 86° W) | 1 | 1 | 1994–2008 | Carricart-Ganivet et al. (2013) |
| <i>Montastraea cavernosa</i> | Puerto Morelos (20° N, 86° W) | 4 | 2 | Not mentioned | Mozqueda-Torres et al. (2018) |
| <i>Dichocoenia stokesi</i> | Puerto Morelos (20° N, 86° W) | 3 | 2 | 1994–2014 | Cruz-Ortega et al. (2020) |
| <i>Dengrogyra cylindrus</i> | Puerto Morelos (20° N, 86° W) | 3 | 7 | 1995–2014 | Cruz-Ortega et al. (2020) |

Table 4. Simple linear regression between calcification rate and sea surface temperature data. PP: *Porites panamensis*; PL: *Porites lobata*; PG: *Pavona gigantea*; DC: *Dendrogyra cylindrus*; DS: *Dichocoenia stokesi*; SS: *Siderastrea siderea*. BLA: Bahía de Los Angeles; BLP: Bahía de La Paz; BAN: Bahía de Bandejas; ISA: Isla Isabel; PMR: Puerto Morelos. EP: Eastern Pacific; C: Caribbean. Significant ($p < 0.05$) values are displayed in **bold**

| Species / site / region | Female data | | | Male data | | | Female and male averaged data | | | | |
|-------------------------|-------------|--------------|----------------|-----------|-----------|----------------|-------------------------------|--------------|----------------|----|---------------|
| | Slope | Intercept | r ² | Slope | Intercept | r ² | Slope | Intercept | r ² | n | p |
| PP / BLA / EP | -0.12 | 4.97 | 0.45 | -0.06 | 1.93 | 0.22 | -0.09 | 2.64 | 0.34 | 15 | 0.02 |
| PP / BLP / EP | -0.69 | 17.71 | 0.38 | -0.50 | 13.59 | 0.22 | -0.59 | 15.48 | 0.34 | 12 | 0.04 |
| PP / BAN / EP | -0.24 | 6.90 | 0.83 | -0.05 | 1.87 | 0.41 | -0.05 | 1.91 | 0.41 | 10 | 0.04 |
| PL / ISA / EP | -0.07 | 2.35 | 0.63 | -0.13 | 4.02 | 0.47 | -0.10 | 3.19 | 0.58 | 7 | 0.04 |
| PG / BAN / EP | -0.40 | 11.71 | 0.75 | -0.37 | 11.16 | 0.23 | -0.39 | 11.64 | 0.44 | 25 | 0.0002 |
| DC / PMR / C | -1.08 | 30.66 | 0.44 | 0.50 | -12.03 | 0.17 | -0.47 | 14.50 | 0.26 | 20 | 0.02 |
| DS / PMR / C | -0.18 | 5.09 | 0.49 | -0.22 | 6.73 | 0.11 | -0.21 | 6.12 | 0.29 | 21 | 0.01 |
| SS / PMR / C | -0.15 | 4.61 | 0.44 | -0.19 | 5.86 | 0.11 | -0.17 | 5.30 | 0.26 | 15 | 0.048 |

reproduction patterns (e.g. brooding or broadcast spawning), and one or several reproductive cycles per year (Table 1).

The fact that female corals are more sensitive to changes in SST than male colonies is relevant in the context of climate change if the current thermal stress trends continue as predicted for all reef areas worldwide (Pandolfi et al. 2011, Alvarez-Filip et al. 2013, Manzello et al. 2017, Hughes et al. 2018). Considering that stony corals are being exposed to increasing SSTs, the first effect of this environmental stress would be a differential decrease in the calcification rate (Wórum et al. 2007, Cooper et al. 2008, De'ath et al. 2009, Saenger et al. 2009, Tanzil et al. 2009, 2013, Cantin et al. 2010, Carricart-Ganivet et al. 2013, Tortolero-Langarica et al. 2017). Here, we show that a reduction in the calcification rate will be more severe in female colonies (Fig. 6).

Energy availability and expenditure are established hierarchically to cover all base metabolism needs in corals (Leuzinger et al. 2012); thus, when a colony experiences a reduction in available energy, reproduction is inhibited to maintain tissue integrity and calcification (Leuzinger et al. 2012). Currently, there is some evidence in the eastern Pacific, Caribbean, and Hawaii that gametogenesis is inhibited when corals experience several and/or severe thermal stress events (e.g. El Niño–Southern Oscillation; Carpizo-Ituarte et al. 2011, Levitan et al. 2014, Hagedorn et al. 2016, Santiago-Valentín et al. 2018). Thus, if thermally stressful conditions continue, coral fecundity could decrease or female corals might have to adjust their energy budgets to compensate for lower calcification rates. Finally, if higher growth rates and/or a lower sensitivity to thermal stress confer advantages to males during recruitment and early community succession, then there might be a bias selection toward male-dominated communities, as suggested by Harrison & Wallace (1990), Holcomb et al. (2012), Cabral-Tena et al. (2013), and Glynn et al. (2017).

5. MISSING PIECES IN THE PUZZLE AND RECOMMENDATIONS FOR FUTURE DIRECTIONS

The sex-associated differences in the sclerochronological traits of stony corals have been detected in coral species with solid and porous skeletons as well as in both spawning and brooding species. The difference in growth rates between sexes is consistent among species from the Caribbean and ETP regions. It would

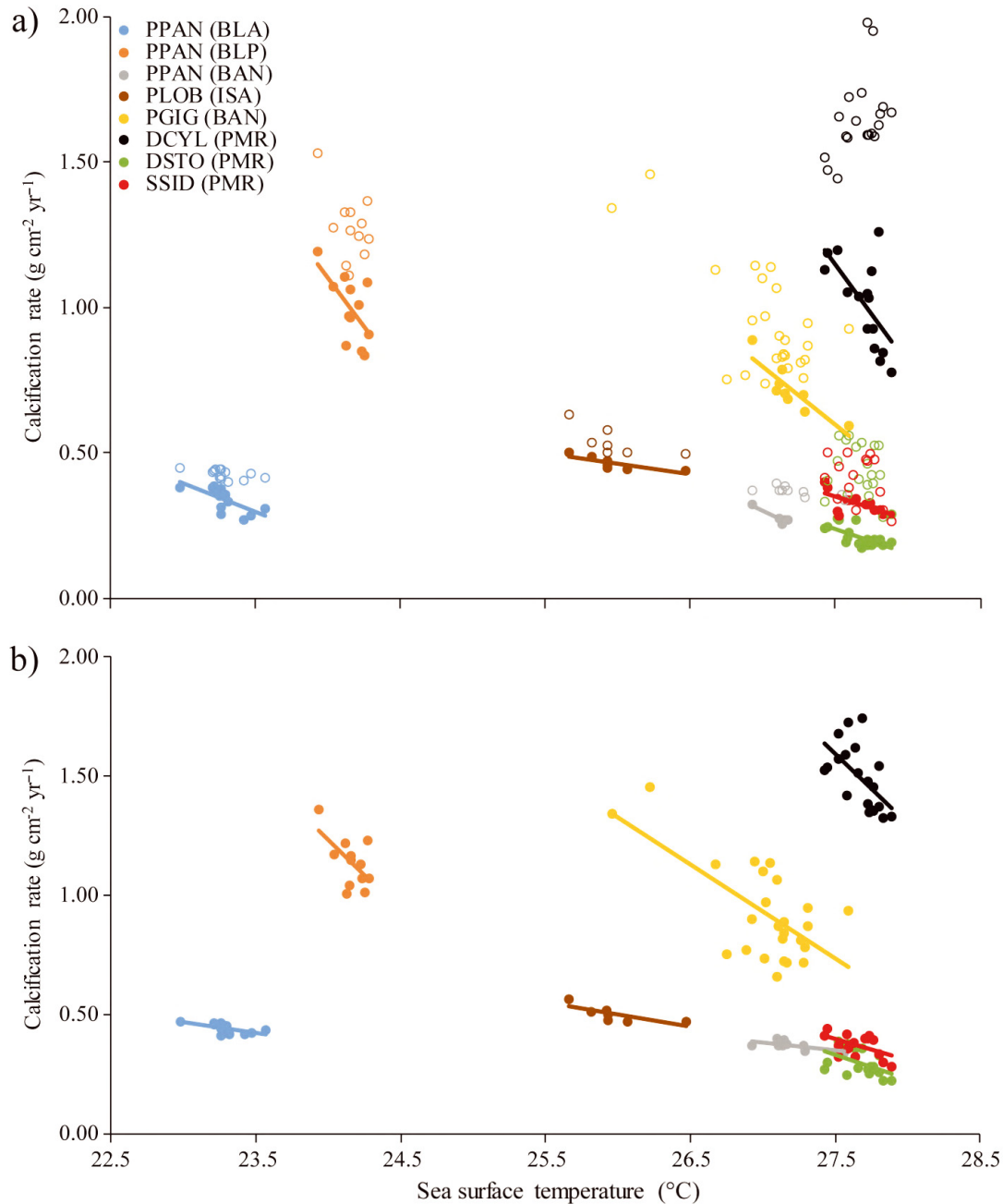


Fig. 6. Mean annual calcification rates as a function of the average annual sea surface temperature. (a) Data split by sex: solid circles: females; open circles: males. (b) Averaged data. PPAN: *Porites panamensis*; PLOB: *Porites lobata*; PGIG: *Pavona gigantea*; DCYL: *Dendrogyra cylindrus*; DSTO: *Dicochoenia stokesi*; and SSID: *Siderastrea siderea*. Sites: BLA: Bahía de Los Ángeles; BLP: Bahía de La Paz; ISA: Isla Isabel; BAN: Bahía de Banderas; and PMR: Puerto Morelos. The color of each line is the same as its data marker color. Data sets collected from Cabral-Tena et al. (2013), Carricart-Ganivet et al. (2013), Tortolero-Langarica et al. (2016, 2017), and Cruz-Ortega et al. (2020)

be interesting to determine whether this pattern is also present in other gonochoric genera of the Caribbean (e.g. *Meandrina*, *Stephanocoenia*), and in other *Porites* corals in the Indo-Pacific, which have been used extensively for paleoclimatic reconstructions and sclerochronological studies (Lough & Barnes 2000, Cooper

et al. 2008, Lough 2008, De'ath et al. 2009, Cantin & Lough 2014).

It would also be interesting to assess whether the sex-associated differences in the growth rates of stony corals are also present in other corals with complex (or mixed) reproductive histories and strategies

such as *Pavona gigantea*, which exhibits sequential cosexuality as in other agariciid species (Glynn et al. 1996, 2000, Santiago-Valentín et al. 2015, Tortolero-Langarica et al. 2017), gynodioecious corals (e.g. *Porites astreoides*; Chornesky & Peters 1987), pseudogynodioecious corals (e.g. *Galaxea* species; Harrison 1988), or protandrous species (e.g. *Stylophora pistillata*; Rinkevich & Loya 1987). Another complication arises from the fact that some coral species have mixed breeding systems, for example, *Dichocoenia stokesi* has been reported as predominantly gonochoric (~83%) with a small percentage of hermaphrodites (~17%) (Hoke 2007). On the other hand, *Dengrogyra cylindrus* has been reported as not strictly gonochoric, with a low portion of the population (~20%) being sequential hermaphrodites (Neely et al. 2018), further complicating any sex-associated differences in the growth rates of these species (which, of course, may be true in other species). The sex allocation theory of Charnov (1982) proposes that colonies are male during early life stages because of the lower energy investment required to produce only sperm, which allows male colonies to invest more energy in growth and survival than female colonies. The energy not invested in female reproduction allows male colonies to lower their risk of mortality during these important initial stages until energy allocation to both female and male functions is sustainable at later life stages. This results in a differential fitness between sexes during the initial life stages (Charnov 1982). Given this context, coral colony size is an important variable in reproduction, as it is delayed in some species until a sufficiently large colony is formed. Thus, a tradeoff between coral reproduction and growth seems to exist, especially in female colonies (Benayahu & Loya 1986, Chornesky & Peters 1987, Holcomb et al. 2012). It would be interesting to compare sclerochronological characteristics during the different life stages of coral species, such as before and after colonies reach sexual maturity or change sex. In addition, it is necessary to verify if the sexual reproduction strategy (e.g. broadcast spawning or brooding) is important during the different life history stages of gonochoric coral species.

To identify potential threats and improve management strategies for coral reef ecosystems, the interpretation of proxies for environmental records based on the skeletons of gonochoric corals should consider how sclerochronological characteristics vary with sex. It is worth mentioning that sex determination in corals is complex and can only be done during a short time window before reproductive events. This becomes particularly problematic in fossil corals or in colonies

that were collected for sclerochronological analysis but where the collection of tissue samples was not considered to identify the sex of the coral (i.e. sex determination is not possible). However, the studies of González-Espinosa et al. (2018) and Pedraza-Pohlenz et al. (2023) offer a plausible alternative. González-Espinosa et al. (2018) and Pedraza-Pohlenz et al. (2023) described sexual dimorphism in 3 skeletal morphological traits (corallite diameter, the number of neighboring corallites, and the density of corallites per unit area) of *Porites panamensis* and *P. lobata* in the southern Gulf of California, which could serve to classify and characterize recent or fossil records correctly. It is worth mentioning that the findings of González-Espinosa et al. (2018) and Pedraza-Pohlenz et al. (2023) were based on only a few sites. Therefore, future research is needed to determine whether the sexual dimorphism reported by these authors is also characteristic of other species and regions. An interesting hypothesis would be whether sexual dimorphism is present in other species due to the apparent advantages of this characteristic.

Another important point is that, to our knowledge, there are only a few studies addressing, considering, or reporting the sex ratio of the populations of gonochoric corals (Szmant 1986, Cabral-Tena et al. 2013). Szmant (1986) mentioned that brooding species tend to skew towards female dominance but that on the other hand, in broadcasters, the sex ratio is close to 1:1. Cabral-Tena et al. (2013) found that the sex ratio of *P. panamensis*, a gonochoric brooder, is close to 1:1 in the Gulf of California. This means that if a large set of coral cores or colonies (>20) is used in a study addressing sclerochronological characteristics of a 1:1 sex ratio population, this would average out the differences in growth variables between sexes. The main problem is that this type of study normally uses few colonies (<5), so the chance of having a skewed analysis towards either sex, and thus committing some misinterpretation of data, is high. This problem will be more acute in populations that have a natural skew towards either sex.

It is also necessary to determine whether the documented differences between sexes in sclerochronological characteristics (Cabral-Tena et al. 2013, Carriac-Ganivet et al. 2013, Tortolero-Langarica et al. 2016, 2017, Mozqueda-Torres et al. 2018, Cruz-Ortega et al. 2020) are present in other reef sites, as they may become a marker to determine the sensitivity and vulnerability of some coral species to climate change. Finally, to improve our understanding of the differential response to environmental stress between scleractinian coral colonies of different sexes and the

potentially disruptive implications for the structure of coral populations, future research should assess whether a sex-associated differential response in coral growth and reproduction among sexes of gonochoric coral species is present with other climate change-associated variables in addition to SST, such as aragonite saturation or reductions in pH.

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